THE ADAPTIVE VALUE OF POLYMORPHISM IN AN ALPINE ANT, *FORMICA NEORUFIBARBIS GELIDA* WHEELER*

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Introduction

Organisms that inhabit alpine tundra must be able to survive and reproduce under extreme environmental conditions. Most of the year the weather is cold, windy, and the ground covered with snow. As the snow melts in the spring, the ground becomes saturated with water and there is considerable run-off. Summers are short and characterized by frequent rains, high solar radiation, and extreme temporal and spatial variations in humidity. Animals that remain on the tundra year round can be expected to have acquired habits and associated structures which enable them to overcome the difficulties of these high altitude conditions.

Of the tundra ant species, *Formica neorufibarbis gelida* is the most abundant and often the only ant species inhabiting the alpine tundra of the Colorado Rockies. According to Gregg (1963), it is the most cold tolerant of all the ant species found in Colorado. Additional adaptations include the ability to nest under rocks (which provide protection from temperature and humidity extremes) and the relatively rapid production of a single brood (from eggs to adult workers and sexual forms) within the short summer season (Taussig, 1962).

During preliminary observations on the ecology of this subspecies, I noticed color differences in the thorax of foragers—some were brownish-black and others red. Both types were found within every colony observed. The foragers with red thoraxes also appeared to be larger in body size than those with darker thoraxes. The possibility that either color or size polymorphism might be associated with adaptation to tundra environments stimulated the work presented in this paper.

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Methods

The general ecology and thorax color of *F. neorufibarbis gelida* were examined at several different alpine tundra sites on the east slope of the Rockies during the summers of 1975 and 1976. Intensive study and data collections were from a single tundra site, Niwot Ridge, located approximately 20 miles northwest of Boulder, Colorado. This area is supervised by the Institute of Arctic and Alpine Research, University of Colorado, and therefore relatively undisturbed by human activities.

Weekly visits were made to the Niwot Ridge study site between June 21 and August 10, 1976. Records were kept of the number and color of foragers, type of food collected, the times of day when foraging took place and where the foragers searched for food. Developmental stages of the brood were observed by turning over rocks near midday, when the brood is brought to the surface of the nest.

Samples of 20 foragers each were taken from various different foraging heights (ground, flowers, and shrubs of heights ranging from 20 cm to one meter) and at different times of the day. Because several environmental factors, including light intensity, temperature and humidity, change in a regular fashion with time of day when the effects of the sun are not obscured by clouds, all collections were made on cloudless days. The samples of foragers were then taken to the laboratory, the color of each individual noted, and its head width measured with a Lietz eyepiece micrometer.

Results

More than 85% of the food collected by the colonies on Niwot Ridge consisted of liquid material from plants. From the beginning of the season through peak flowering time, most of the food was nectar from flowers, primarily that of *Acomastylis rossii*. Later in the season, major foraging activity occurred on the stems of plants, where the ants sucked liquids from the area around the axil. Of the other types of food collected, seeds comprised less than 5% and dead insects about 10% of the diet. Regardless of the abundance of food, once the brood had matured, all foraging ceased for the season.

Head width measurements of foragers with red thoraxes and of those with dark thoraxes were plotted according to frequency

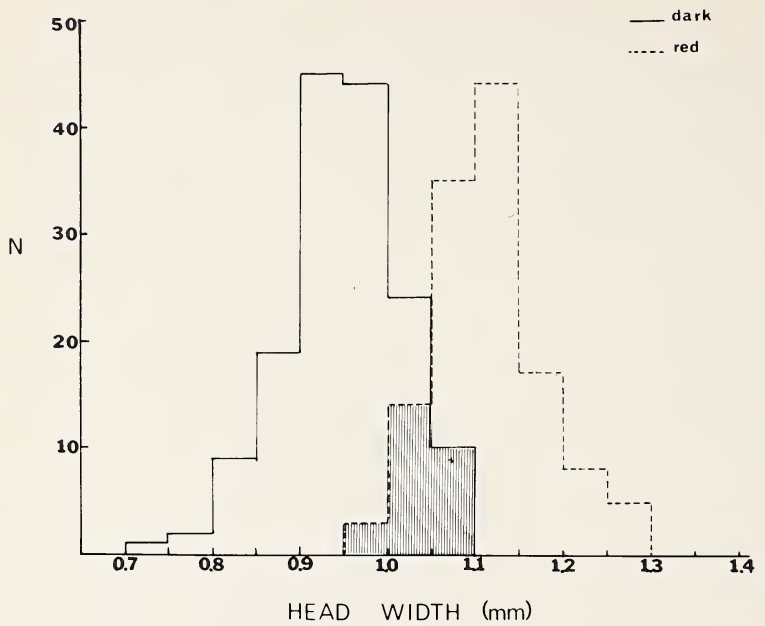

Figure 1. Frequency distribution of forager head width. The solid line is of 154 foragers with dark thoraxes; the dotted line is of 126 foragers with red thoraxes. The population appears to be dimorphic for both color and size.

of size classes. These are shown in Figure 1. A total of 280 individuals are represented, with 154 dark and 126 red. Mean head width of the dark forms is 0.944 ± 0.067; of the red forms, 1.111 ± 0.065 mm. A t-test of the two means indicates the differences are highly significant ($p < 0.005$); the population is dimorphic for both color and size.

The mean head width for each sample of 20 individuals was calculated and tested for degree of correlation with foraging height at which the sample was collected and time of day. No significant correlations were found to exist between foraging height and head width. There was, however, a significant positive correlation between mean head width and the time of day that the sample was collected. This relationship is shown in Figure 2. The correlation coefficient, 0.848, is significant at $p < 0.005$.

Because no correlation was found between forager size and foraging height (which should reflect different temperatures and humidities at a given time of day), the observed change in forager size and color with time of day is likely to be the effect of changes in the amount of solar radiation. This interpretation is strengthened by the fact that all of the samples taken in June, when light intensity is lower than in later months (Taussig, 1962), lie below the line of best fit.

Discussion

Each colony of *F. neorufibarbis gelida* consists of a mixture of both red and dark foragers, the red tending to be larger in size than the dark. As foraging progresses through the morning, the proportion of large, red foragers increases. It seems likely that the small, dark forms have an advantage early in the day, in that they are able to warm up more quickly so that foraging can begin. As solar radiation increases throughout the morning, the advantage shifts to the larger, red forms because a larger body tends to heat up more slowly and the red color probably reflects more solar radiation than would a dark color. A colony made of both forms of foragers is able to withstand greater variations in solar radiation and therefore utilize more foraging hours per day than a colony containing only one form or the other. The lower foraging limit of this subspecies is about 12° C soil surface temperature (Taussig, 1962); the upper limit is not known because foraging has never been observed to cease during the heat of midday. Taussig (1962) reports active foraging at a soil surface temperature of 52° C.

Both small body size and dark color are characteristics of other high altitude insects and considered adaptations to cold temperatures (Mani, 1962). Another characteristic is that the activities of these insects are usually restricted to cold temperatures and they actually show a drop in activity during midday (Mani, 1962). The colonies of *F. neorufibarbis gelida,* however, were never observed to decrease their foraging activities during high environmental temperatures, a feature perhaps due to the presence, in these colonies, of not only the small, dark individuals typical of alpine environments, but also the large, red individuals.

It is concluded from this study that the color and size differences observed in *F. neorufibarbis gelida* enable each colony to utilize a greater range of environmental conditions for foraging than if

they were of a single size and color. The resultant increase in number of foraging hours each day enables a colony to quickly raise a brood to maturity within the very short summer season in alpine tundra environments.

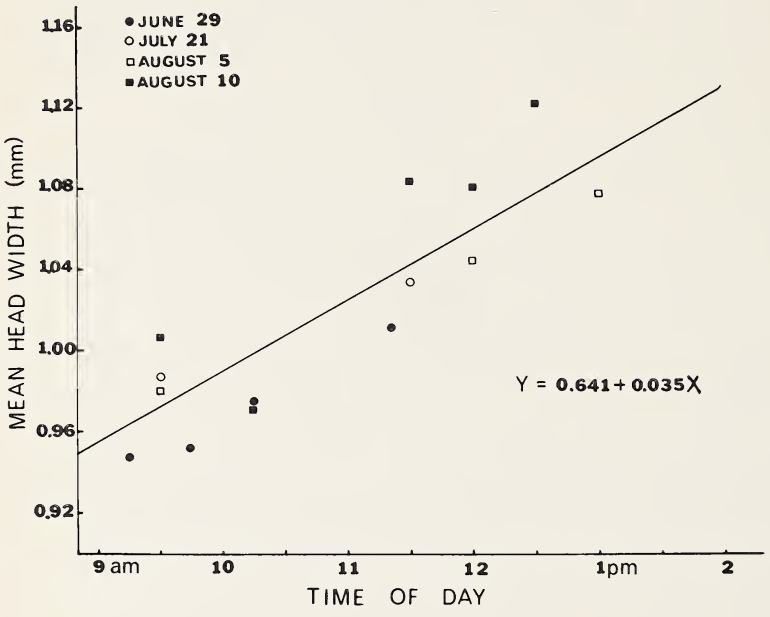

Figure 2. The mean head width of each sample of foragers shown as a function of time of day the sample was taken. Each point is the mean of 20 individuals in a sample. The correlation coefficient, $r = 0.848$, is significant at $p < 0.005$.

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